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Effects of Strawbedding on Physiological Responses to Stressors and Behavior in Growing Pigs

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DE JONG, I. C., E. D. EKKEL, J. A. VAN DE BURGWAL, E. LAMBOOIJ, S. M. KORTE, M. A. W. RUIS, J. M. KOOLHAAS AND H. J. BLOKHUIS. *Effects of strawbedding on physiological responses to stressors and behavior in growing pigs*. *PHYSIOL BEHAV* 64(3) 303–310, 1998.—To study the effects of environmental enrichment on physiological responses to stressors and behavior in growing pigs, pigs were housed in either a poor environment (standard farrowing pens followed by standard rearing and fattening pens) or in an enriched environment (larger farrowing pens followed by larger rearing and fattening pens, provision of straw). Body temperature, heart rate and salivary cortisol were measured during baseline conditions and in response to relocation, isolation and restraint. Pigs housed in the poor environment performed more manipulative social behavior directed to penmates than pigs housed in the enriched environment. Physiological responses to the stressors were the same for enriched- and poor-housed pigs. Surprisingly, enriched-housed pigs had significantly higher baseline salivary cortisol concentrations, especially at 14 and 17 weeks of age. Moreover, enriched housed pigs had a lower baseline body temperature at 17 weeks of age. Thus, provision of straw has an effect on behavior, baseline HPA-axis activity and baseline body temperature in growing pigs. © 1998 Elsevier Science Inc.

Environmental enrichment Pigs' behavior Cortisol Body temperature Heart rate

In modern pig husbandry, growing pigs are housed under intensive conditions in a barren and restricted environment. Behavioral studies show that such intensive housing conditions may hamper the development of normal behavior patterns and have negative effects on pig welfare (2,29,30).

Several studies have compared the behavior of pigs housed under intensive conditions with the behavior of pigs housed in a more enriched environment, such as pens provided with substrate (12) or pens with increased floor space and substrate (2,3,29). Pigs housed in these enriched pens spent more time in exploration and had more diverse behavior patterns compared to pigs housed under intensive conditions (2,12,29) and showed less restlessness during rearing and when adult (29). Enriched housed pigs showed less manipulative social behaviors such as nosing, biting and massaging littermates (2,3,29). Poor rearing conditions disturb the development of appropriate social skills; piglets thus housed develop abnormal agonistic behavior (29) and behave more aggressively (6) than pigs housed in an enriched environment. Moreover, the subordinate pigs reared in a poor environment showed delayed estrus development, decreased weight gain, and a prolonged increase in cortisol after tethering compared to enriched reared pigs (6).

Studies have shown that space restriction (1,20,24) or regular

handling (14) not only affect behavioral but also physiological responses in growing pigs. Although it is known that environmental enrichment improves pig welfare by limiting manipulative social behavior and improving social skills (2,3,6,29), it is unknown if physiological responses of pigs to stressors are affected by environmental enrichment. Therefore, in the present experiment we studied the effect of environmental enrichment on the behavior and physiological responses to acute stressors in growing pigs.

We housed half of the pigs in standard intensive farrowing and fattening pens (referred to as "poor" environment). The remainder was housed in larger farrowing and fattening pens which were supplied with straw (referred to as "enriched" environment). Body temperature, heart rate and salivary cortisol were measured during baseline conditions and in response to relocation, isolation, and restraint. Behavior was observed in the home pen and during a confrontation test with an unfamiliar pig.

MATERIALS AND METHODS

Animals and Housing

Pigs (Great Yorkshire × (Great Yorkshire × Dutch Landrace) used in this experiment were housed in either an enriched envi-

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ronment or in a poor environment from birth to slaughter. Three successive replicates of sixteen pigs were used in the experiment. Within each replicate, two groups of four pigs were assigned to the enriched (E) environment and two groups of four pigs were assigned to the poor (P) environment.

Four sows (Great Yorkshire \times Dutch Landrace) per replicate bred the piglets used in this experiment. One week before the expected date of farrowing, the sows were housed in the farrowing pen. E piglets were born in farrowing pens (7.2 m²) with a concrete lying area covered with straw (1.75 \times 2.4 m) and a concrete slatted area (1.25 \times 2.4 m). P piglets were born in standard farrowing pens where the sows were crated (3.1 m², half concrete area, half metal slats). Castration of male piglets, teeth clipping, ear tattooing and tail docking were carried out at 3 days of age, following standard animal husbandry procedure at the experimental farm.

Piglets were weaned at 4 weeks of age and six piglets per sow (three barrows, three gilts) were randomly selected for use in this experiment. E piglets stayed in the same pen at weaning; the sow and not-selected piglets were removed. At weaning, P piglets were brought to the same room as the E piglets and housed in fully slatted pens (3 m²) with their selected littermates. At 6 weeks of age, one barrow per group was selected for implantation of a biotelemetric transmitter (see below).

At 10 weeks of age four experimental pigs per sow (one barrow with a transmitter and one barrow and two gilts without) were selected. E pigs were relocated to enriched fattening pens (4.64 m²) with half concrete area covered with straw and half concrete slats. Fattening pens were in the same building but in another room. P pigs were relocated to poor fattening pens (3.36 m²) with half concrete lying area and half concrete slatted floor. E and P fattening pens were in the same room. All pens were cleaned daily and fresh straw was provided in the E pens in the morning.

Throughout the experiment, water and food were available ad lib. Environmental temperature was kept between 21–23°C in each room. Artificial lights were on from 0600–1800 hours, with no daylight visible in the rooms.

Individual pigs could be recognized by a plastic ear tag, an ear tattoo, and a number painted on their back. All pigs were accustomed to by weekly handling to the experimenter from 6 weeks of age to avoid unwanted stress reactions at saliva sampling.

Physiological Measurements

Body temperature and heart rate measurements. Body temperature and heart rate were measured by active radiotelemetry using implantable biotelemetric transmitters. At 6 weeks of age, biotelemetric transmitters (model TA10CTA-D70, DataSciences, St. Paul, MN, USA) were implanted surgically in 12 barrows (one barrow per group) under complete anesthesia. Pigs were food-deprived for 12 h, sedated with azaperone intramuscularly (i.m.) (1 cc/2 kg, Stresnil®, Janssen Pharmaceutica, Tilburg, The Netherlands) and anesthetized with metomidate hydrochloride i.v. (2.5 cc/5 kg, Hypnodil®, Janssen Pharmaceutica). The transmitter was implanted in the peritoneal cavity by making a longitudinal incision just caudal to the thorax. One electrode lead was fixed to the caudal surface of the xiphoid process. The other lead was subcutaneously extended on the thorax toward the cranial insertion of the sternohyoid muscle and sutured in place. After recovery from anesthesia, pigs were put back in their home pen and treated with antibiotics (Ampicillin® 20%, AUV, Cuijk, The Netherlands) for 5 days; the experiments started 3 weeks later.

Frequency-modulated heart rate and body temperature signals were received by antennae (model RLA2000, DataSciences) above the pen. Data were processed, stored, and analyzed with a personal computer using a specialized data analysis system (LabPro version

TABLE 1
ETHOGRAM SHOWING THE BEHAVIORAL MEASURES OF THE HOME PEN RECORDINGS

Behavior	Definition
Eating	Time spent with the head in the feeder
Walking	Walking through the pen
Running	Trotting, galloping through the pen
Explore object	Sniffing, touching or pushing objects
Explore substrate	Rooting, sniffing, touching the substrate
Explore pen	Rooting, sniffing, touching the walls or ground of the pen (except substrate and objects)
Nosing	Sniffing with the nose any part of another pig
Massaging	Rubbing any part of another pig
Nibbling	Nibbling any part of another pig
Other	All other behaviour
Posture	Definition
Standing	Standing, walking, running on four legs
Lying	Lying on side or sternum
Sitting	Standing on fore-legs, hind quarter on the floor

3.1, DataSciences). Body temperature and heart rate were sampled for 20 s at 1-min intervals during testing.

Saliva collection and cortisol analysis. Saliva was collected from all pigs by allowing the pigs to chew on two large cotton buds until they were thoroughly moistened (about 30–60 s per sample). The buds were placed in tubes and centrifuged 10 min at 400 \times g. Saliva samples were stored at –20°C until analysis. Cortisol concentration in saliva samples was determined using a solid-phase radioimmunoassay kit (Coat-a-Count Cortisol TKCO, Diagnostic Products Corporation, Apeldoorn, The Netherlands) modified for pig salivary cortisol (26).

Weight development. Pigs were weighed at weaning (4 weeks of age), relocating (10 weeks of age), and slaughter (27 weeks of age).

Adrenal weight. At slaughter the adrenals were removed and weighed. Weight of both adrenals was averaged and expressed as percentage of body weight.

Home Pen Behavior

Home pen behavior was studied at 21 weeks of age. Behavior was recorded on videotape during the light period (0600–1800 hours) on 4 successive days. Duration and frequency of the behavioral elements as described in Table 1 were scored continuously per pig using the Observer program (Noldus, Wageningen, The Netherlands).

Agonistic Behavior in Confrontation Test

Agonistic behavior was studied in a confrontation test. At 26 weeks of age, pigs were confronted pairwise in a test pen in another room. Two pigs of the same treatment and sex but from different pens were randomly chosen and brought to the test pen (1.75 \times 2.4 m) with a concrete floor. Water was available ad lib.; no food was available. Behavior was recorded on videotape for 4 h (1000–1400 hours). Thereafter, the pigs were taken back to their home pen. Agonistic behavior was classified as described by Jensen et al. (19). Duration and frequency of the behavioral elements as described in Table 2 were scored continuously per pig using the Observer program (Noldus).

TABLE 2
ETHOGRAM OF THE BEHAVIOR SCORED IN THE CONFRONTATION TEST

Behaviour	Definition
<i>States (duration scored)</i>	
Lying	Lying inactive on side or sternum
Standing inactive	Standing inactive, apparently doing nothing
Agonistic	All agonistic behavior, i.e. pushing, lifting, biting, nosing, knocking (see description of the scored events)
Other	All other activities than lying, standing inactive, agonistic
<i>Events (frequency scored)</i>	
Knock	A rapid thrust upwards or sideways with the head or snout to any part of the body, including the head
Bite	Bites directed at all parts of the body
Push	Pushing the shoulders against the other pig, throwing the head against the neck, flanks or head of the other
Lift	Pushing the snout under the body of the other pig and lifting it up
Nose-to-nose	Sniffing or shortly touching the nose or head of the other pig
Ano-genital nosing	Sniffing or shortly touching the genital region of the other pig
Nose-to-body	Sniffing or shortly touching the body of the other pig, except the ano-genital region or the head
Submissive	The pig moves away from the other pig rapidly with head high. Occurs only after a fight

Stressors

Relocation. At 10 weeks of age, four pigs per group were selected (see above). At 1200 hours, these pigs were randomly taken out of their pen, weighed, and immediately put in a fattening pen in another room with their littermates. Saliva samples were taken at 45 and 5 min before and at 5, 15, 30, 60, 90, and 120 min after relocation. Body temperature and heart rate of one barrow per group was measured from 45 min before relocation until 120 min after relocation.

Isolation. At 14 weeks of age, pigs were randomly subjected to 1 h isolation without water and food in a test pen (1.45×1.45 m, no substrate) in a separate room. There was no visual, auditory and olfactory contact with other pigs. The isolation tests were carried out between 0930 and 1400 hours. Behaviors and vocalizations were recorded on videotape during the isolation period and analyzed using the Observer program (Noldus). The duration of the following behaviors was scored: 1) walking; 2) standing; 3) sitting; 4) exploring, i.e., sniffing, chewing or nosing the pen or the floor; and 5) lying. Frequency of vocalization bouts was scored using the following classification: 1) grunts: all low-pitched vocalizations; 2) squeals: all high-pitched vocalizations. Saliva samples were taken at 45 and 5 min before and at 5, 15, 30, 60, 90, 120, 150, and 180 min after the beginning of the test. Body temperature and heart rate of one barrow per group was sampled from 45 min before until 180 min after the start of the test.

Restraint. At 17 weeks of age the pigs were randomly subjected to 15 min restraint by using a nose snare; this procedure is commonly used for immobilization in pig husbandry. Pigs were individually relocated from their home pen to a separate test pen in another room and immediately snared by putting a rope around the upper jaw for 15 min. Tests were carried out between 1100 and 1300 hours. Vocalization bouts during testing were recorded and their frequency scored using the classification as described for the isolation test. Saliva samples were taken at 45 and 5 min before and at 15, 30, 60, 90, 120, 150, and 180 min after the start of the test. Heart rate and body temperature of one barrow per group was measured from 45 min before until 180 min after the start of the test.

Data Reduction and Statistical Analysis

Body temperature and heart rate were averaged over 15-min periods before and after the start of the stress procedure. Increase or decrease in body temperature or heart rate was determined by

comparing the 15-min averages during and after the stress test with the 15-min baseline value and by calculating the peak height compared to the baseline value. Increase in salivary cortisol concentrations was determined by comparing salivary cortisol concentrations to the baseline value at $t = -5$ min. Total response of the HPA-axis was expressed as the area under the response curve (AUC), calculated as the area above the baseline value at $t = -5$ min.

Changes in physiological parameters within E and P groups were determined for each stressor using a paired *t*-test. Differences in weight, adrenal weight, and cortisol concentration between the treatments were analyzed with a mixed ANOVA model with treatment, replicate, and sex as fixed effects in the model and group entered as random effect. Components were estimated with Restricted Maximum Likelihood Model (REML) procedure (11). No effects of replicate or sex or interaction between replicate and sex were found, and these factors were excluded from the model. Differences in body temperature and heart rate were analyzed using the REML procedure with treatment and replicate as fixed effects. The factor replicate did not significantly contribute to the variance and was excluded from the model. Correlations between variables were determined using the Spearman Rank Correlation test (11).

A general ANOVA was used to assess differences in the relative frequency of behavioral elements in the home pen between E and P pigs. The replicate factor was excluded from the model as it did not significantly contribute to the variance. The same method was used to test for differences in the frequency of behavioral elements scored in the social confrontation test. Sex and interaction factors were initially included in the model, but because these did not significantly contribute to the variance, they were deleted from the model in the final analyses. Differences or correlations were considered significant if $p < 0.05$.

RESULTS

Home Pen Behavior

E pigs differed in their home pen behavior from P pigs. E pigs spent less time nibbling ($p < 0.001$), massaging ($p < 0.05$), and exploring the pen ($p < 0.01$), but more time running ($p < 0.05$) and exploring the substrate ($p < 0.01$) than P pigs (Fig. 1a). E pigs did not differ significantly from P pigs in duration of standing, lying, and sitting.

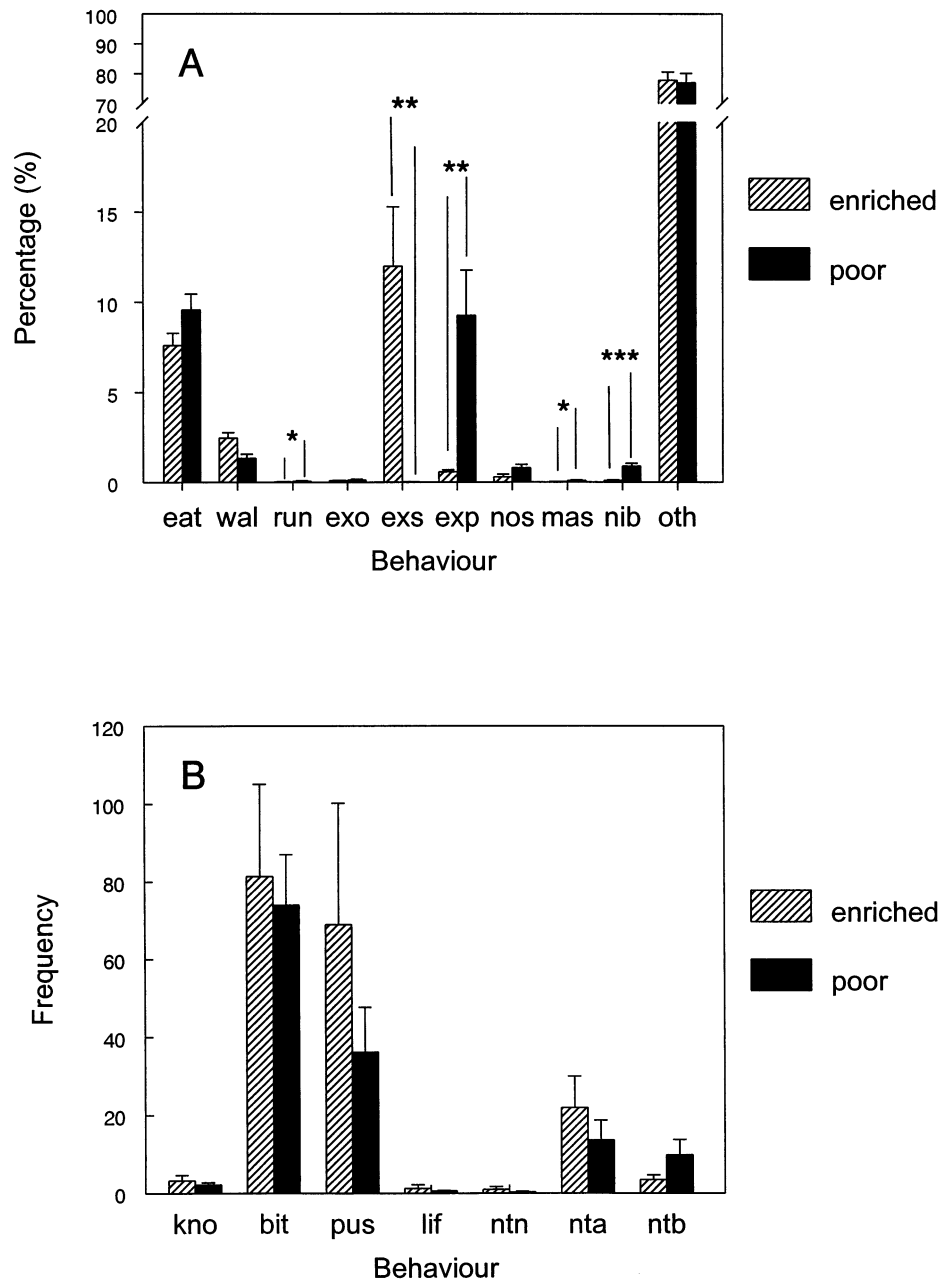


FIG. 1. (A) Relative duration of behavior (mean \pm SEM; $n = 24$ per treatment) scored during the home pen observations for pigs housed in the enriched and poor environment. nib = nibbling; eat = eating; exo = explore object; exs = explore substrate; exp = explore pen; wal = walking; run = running; mas = massaging; nose = nosing. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. (B) Frequency of agonistic behavioral elements (mean \pm SEM; $n = 12$ pairs per treatment) scored in the confrontation test for pigs housed in the poor and enriched environment. kno = knock; bit = bite; pus = push; lif = lift; ntn = nose-to-nose; nta = ano-genital nosing; ntb = nose to body.

Agonistic Behavior in Confrontation Test

When pigs were confronted with an unfamiliar pig in a new pen, P pigs spent more time exploring the new environment than E pigs ($p < 0.05$; $33.4 \pm 4.3\%$ vs. $21.6 \pm 2.9\%$ for P and E pigs, respectively). E pigs spent more time ($p < 0.05$) lying down ($61.2 \pm 3.7\%$ vs. $72.2 \pm 2.8\%$ for P and E pigs, respectively). A high variation in the frequency of scored agonistic elements was observed between pairs. There were no significant differences in

the frequency of the agonistic behavioral elements between the treatments (Fig. 1b).

Responses to Acute Stressors

Relocation

Body temperature. Body temperature significantly increased by 0.5°C above baseline for at least 120 min after relocation for both

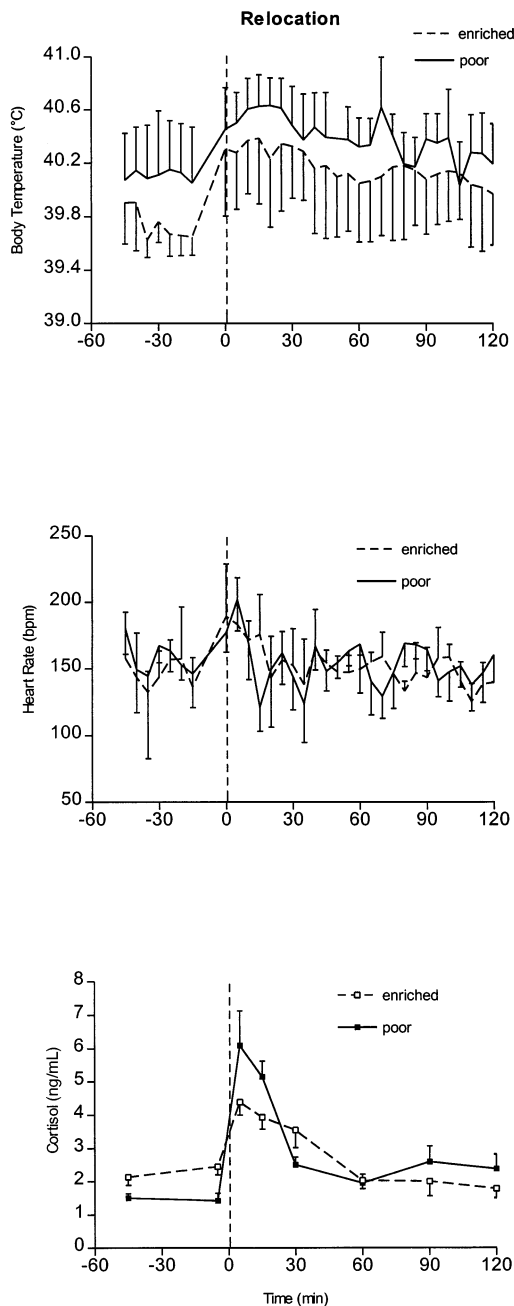


FIG. 2. Acute response of body temperature (mean \pm SEM of $n = 6$ per treatment; upper panel), heart rate (mean \pm SEM of $n = 6$ per treatment; middle panel) and cortisol (mean \pm SEM of $n = 24$ per treatment; lower panel) to relocation at $t = 0$ min. For significant differences between the treatments, see Results.

experimental groups ($p < 0.05$ for E and P pigs) (Fig. 2, upper panel). Fifteen-minute averages of body temperature and body temperature increase after relocation did not differ significantly between E and P pigs.

Heart rate. Heart rate frequency significantly increased after relocation ($p < 0.05$ for E and P pigs), with all pigs reaching a peak between 0 and 7 min after relocation. Heart rate frequency showed large variation after relocation (Fig. 2, middle panel).

Fifteen-minute averages of heart rate and heart rate increase did not differ significantly between E and P pigs.

Cortisol. Cortisol significantly increased after relocation ($p < 0.001$ for E and P pigs), reached its peak level at $t = 5$ min, and decreased thereafter (Fig. 2, lower panel). E pigs had a significantly higher baseline cortisol concentration at $t = -5$ min ($p < 0.05$). At $t = 15$ min P pigs had a significantly higher peak ($p < 0.05$). However, treatments did not differ significantly in the area under the response curve after relocation.

Correlations. Increases in body temperature, heart-rate frequency and salivary cortisol after relocation were not correlated.

Isolation

Body temperature. After a short and very slight increase, body temperature significantly ($p < 0.05$ for E and P pigs) decreased during isolation for both experimental groups; mean decrease during the last 15 min of isolation was $0.64 \pm 0.23^\circ\text{C}$ for P pigs and $0.49 \pm 0.20^\circ\text{C}$ for E pigs (Figure 3, upper panel). Absolute 15 min body temperature averages and body temperature decrease did not differ significantly between E and P pigs.

Heart rate. Heart rates increased significantly after isolation ($p < 0.05$ for E and P pigs) and decreased during the isolation period almost to baseline value (Fig. 3, middle panel). Fifteen-minute averages of heart rate and heart rate increase did not differ significantly between E and P pigs.

Cortisol. Salivary cortisol significantly increased after isolation and reached its peak level at 15 min after the start of the isolation for both treatments (E pigs: $p < 0.05$; P pigs: $p < 0.001$). Cortisol remained high during the isolation and declined after the end of the isolation period (Fig. 3, lower panel). Salivary cortisol concentration was significantly higher for the E pigs before testing: $t = -45$: $p < 0.0001$; $t = -5$: $p = 0.001$ and during testing, at $t = 5$ ($p = 0.05$) and $t = 60$ ($p < 0.05$). Salivary cortisol also was higher after isolation for the E pigs: $t = 90$: $p < 0.01$; $t = 180$: $p < 0.05$ (Fig. 3, lower panel). Peak height and area under the response curve did not differ significantly between E and P pigs.

Behavior and vocalizations. E and P pigs did not differ in duration of behavioral elements and number of vocalizations during isolation (data not shown).

Correlations. Body temperature and heart rate response during isolation were positively correlated or tended to be correlated: first 15-min epoch: $R = 0.70$, $p < 0.05$; second 15-min epoch: $R = 0.60$, $p < 0.10$; third 15-min epoch $R = 0.68$, $p < 0.05$; fourth 15-min epoch: $R = 0.60$, $p < 0.10$.

Restraint

Body temperature. Before restraint, P pigs had a significantly higher ($p < 0.001$) body temperature than E pigs (P pigs: $40.27 \pm 0.08^\circ\text{C}$; E pigs: $39.69 \pm 0.13^\circ\text{C}$). Body temperature increased significantly (E pigs: $p < 0.01$; P pigs: $p < 0.05$) during and after the restraint until 0.5°C above baseline level for both treatments at 25 min after the start of the stressor (Fig. 4, upper panel). Fifteen-minute averages of absolute body temperature values differed during the restraint test: P pigs had a significantly ($p < 0.01$) higher body temperature than E pigs (P pigs: $40.45 \pm 0.10^\circ\text{C}$; E pigs: $40.03 \pm 0.06^\circ\text{C}$). Although the body temperature of P pigs remained higher after the restraint, the difference was not significant (Fig. 4, upper panel). The increase in body temperature compared to baseline level did not significantly differ between E and P pigs.

Heart rate. Heart rate frequency increased at the beginning of the restraint (E pigs: $p < 0.05$; P pigs: $p = 0.10$, n.s.) but immediately decreased until baseline level during the restraint (Fig. 4, middle panel). Fifteen-minute averages of heart rate and

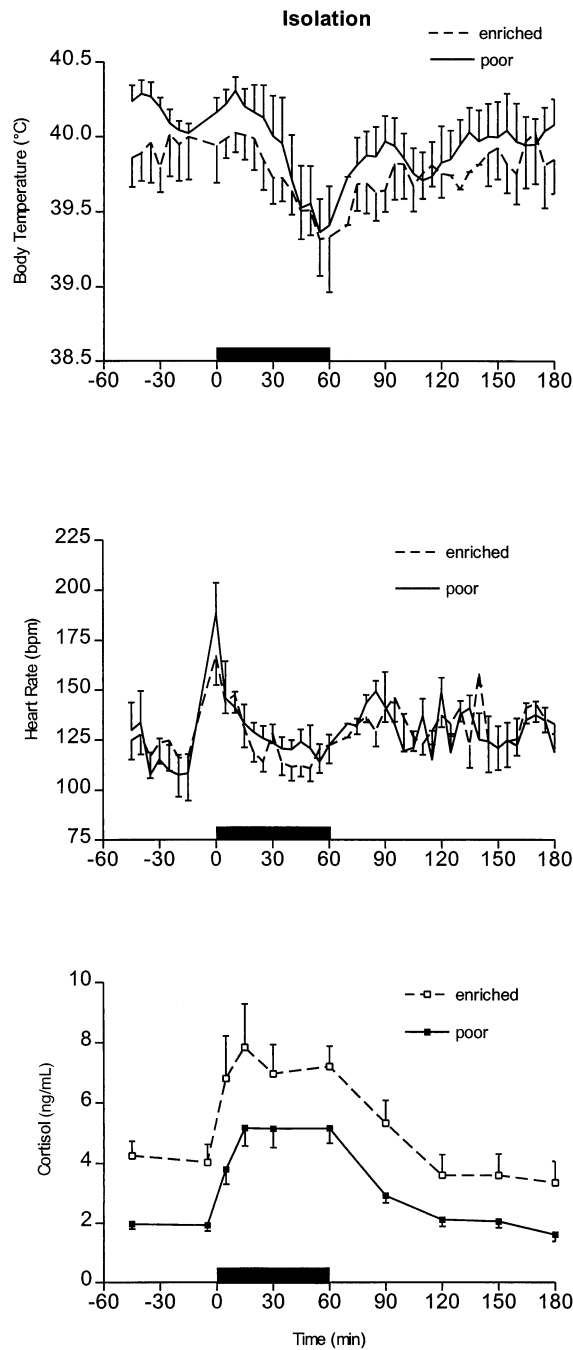


FIG. 3. Acute response of body temperature (mean \pm SEM of $n = 6$ per treatment; upper panel), heart rate (mean \pm SEM of $n = 6$ per treatment; middle panel) and cortisol (mean \pm SEM of $n = 24$ per treatment; lower panel) to isolation. Isolation from 0–60 min. For significant differences between the treatments, see Results.

decrease in heart rate did not differ significantly between E and P pigs.

Cortisol. Cortisol significantly (E pigs: $p < 0.01$; P pigs: $p < 0.001$) increased until 30 min after the beginning of the restraint and did not return to baseline level before $t = 90$ min. Cortisol concentration was higher for E pigs before, during, and after the

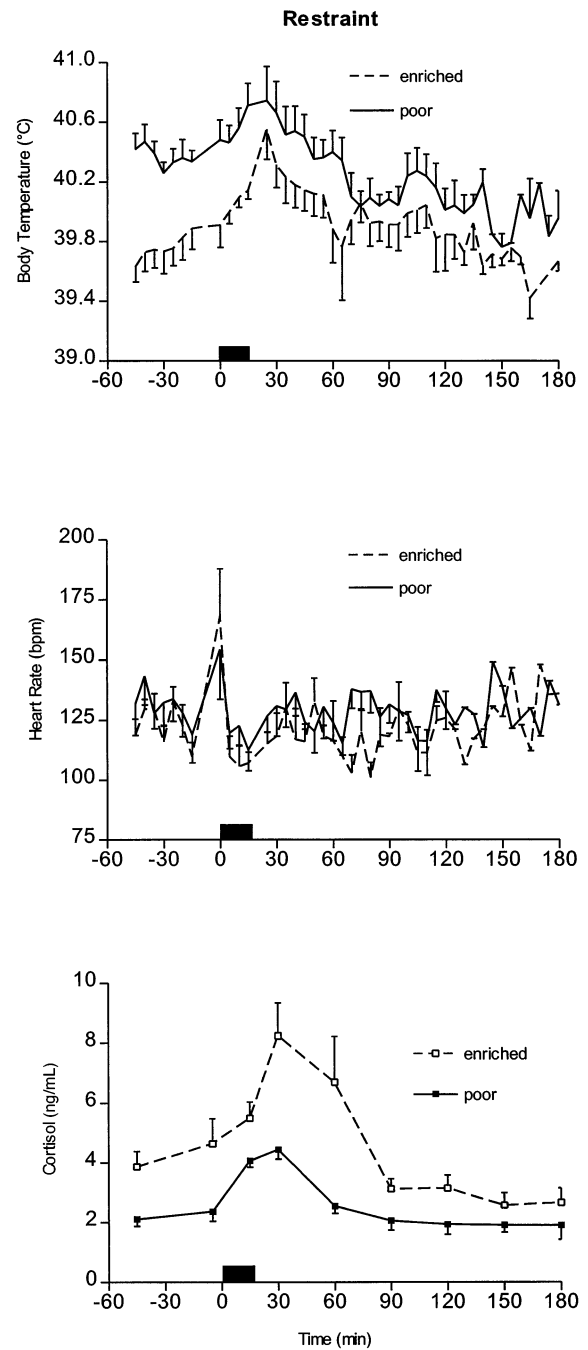


FIG. 4. Acute response of body temperature (mean of $n = 6$ per treatment; upper panel), heart rate (mean of $n = 6$ per treatment; middle panel) and cortisol (mean \pm SEM of $n = 24$ per treatment; lower panel) to restraint. Restraint from 0–15 min. For significant differences between the treatments, see Results.

restraint (Fig. 4, lower panel). E pigs had a significantly higher cortisol at $t = -45$, $t = -5$, $t = 15$, $t = 30$, $t = 60$ ($p < 0.05$), and $t = 120$ ($p < 0.05$). E and P pigs did not differ in peak level and area under the response curve.

Vocalizations. E pigs squealed significantly ($p < 0.01$) more than P pigs (E pigs: 169 ± 12 ; P pigs: 112 ± 13).

Correlations. Body Temperature, heart rate and cortisol responses to restraint were not correlated.

Weight Development

E and P pigs did not differ significantly in weight at 4 weeks of age (6.5 ± 0.2 kg vs. 6.7 ± 0.2 kg), 10 weeks of age (24.5 ± 0.7 vs. 22.6 ± 0.7 kg) and 27 weeks of age (121.2 ± 2.2 kg vs. 110.2 ± 1.9 kg for E and P pigs, respectively).

Adrenal Weight

Adrenal weights of E and P pigs did not differ significantly ($2.0 \pm 0.6 \times 10^{-3}$ vs. $1.6 \pm 0.2 \times 10^{-3}$ % of live-weight, respectively).

DISCUSSION

The present study shows that the provision of straw affects both behavior and physiology in growing pigs. E pigs showed less manipulative social behaviors in the home pen than P pigs at 21 weeks of age, which confirms the results of previous studies (2,3,29). Surprisingly, E pigs had higher baseline cortisol concentrations and a lower baseline body temperature than P pigs. The physiological responses to the stressors did not differ between E and P pigs.

Behavior

E pigs performed less nibbling, massaging and nosing of penmates than P pigs at 21 weeks of age, confirming the results of previous studies (2,3,15,29). Both E and P pigs spent the same time exploring, but P pigs mainly explored the pen, whereas E pigs mainly explored the substrate. The exploration of the pen may be less satisfying than the exploration of substrate, and it has been suggested that because of the lack of suitable material for exploration, P pigs redirect their explorative behavior to the penmates (2,29). The increased amount of manipulative social behavior in P pigs may be injurious to penmates and may eventually lead to cannibalism (2,3), which has obvious negative implications for pig welfare.

In the confrontation test, time spent in exploration was higher for P than E pigs. An increased amount of exploration of novel objects by P pigs than E pigs was shown before (24,30), possibly because P pigs have an unsatisfied motivation for exploration (30). During the isolation test in this experiment, E and P pigs did not differ in the time spent in exploration; however, the stress caused by isolation may have reduced the motivation of the pigs to explore the new environment. Because the duration of the confrontation test was longer, the stress caused by the new environment and the unfamiliar pig may have reduced the motivation to explore in the beginning of the test but not during the latter part of the test.

Although previous work shows that P pigs are more aggressive and show more deviant agonistic behavior than E pigs (6,29), similar differences were not detected in this study. However, we did not determine the social status of the pigs in the present experiment. Previous research showed that subordinate P pigs were more aggressive (6) and that P pigs have more problems in establishing a dominance hierarchy (6,22).

Physiology

Differences in baseline cortisol concentration between E and P pigs, especially at 14 and 17 weeks of age, show that provision of straw has an effect on hypothalamo-pituitary-adrenal (HPA)-axis regulation. Cortisol concentrations in saliva of P pigs were within

the same range as has been found previously for pigs housed under similar conditions (10,26). Higher baseline cortisol concentrations are often associated with chronic stress (6,28,32). Surprisingly, E pigs had a significantly higher baseline cortisol concentration than P pigs, whereas previous studies showed that welfare is improved in E pigs (2,6,29). However, as suggested previously (18,27,32), the assessment of stress should not be based on baseline cortisol measurements only. In addition, a prolonged cortisol increase in response to stressors, increased adrenal weight, and the performance of abnormal or injurious behavior are indicative of chronic stress (13,17,28,32). Except from the higher baseline cortisol concentrations, physiological and behavioral observations in this experiment do not indicate that E pigs were chronically stressed. E pigs did not show a prolonged cortisol increase in response to stressors, and adrenal weight did not differ between E and P pigs. Moreover, manipulative social behavior was decreased in E pigs.

Differences in baseline cortisol concentration between E and P pigs may be ascribed to differences in HPA-axis activity. Rat studies have shown that corticosteroid hormones bind to two types of receptors in the brain: the glucocorticoid receptor (GR) and the mineralocorticoid receptor (MR). The ability of an animal to respond adaptively to its environment is dependent on the balance between MR and GR function (7,8,21,25); a disturbed balance may lead to reduced or enhanced responsiveness to the environment and alter behavioral adaptation (7,21). Therefore, it is important to know if E or P pigs have a disturbed MR/GR balance. Studies on MR and GR concentration and function in E and P pigs are needed to give further information about underlying mechanisms.

The observed differences in baseline cortisol concentration may also be ascribed to differences in circadian rhythm in cortisol between E and P pigs. In addition to the light period, other external cues, such as the daily provision of fresh straw for E pigs, can affect the circadian rhythm (31). However, stress can also flatten the affect the circadian rhythm in cortisol (e.g., 4, 16, 26), which may explain the difference in baseline cortisol concentration between the treatments.

P pigs had a higher body temperature than E pigs. Stress can affect the body temperature rhythm and the body temperature level (9). The differences in baseline body temperature may also be explained by differences in circadian rhythms, as suggested for the differences in baseline cortisol concentration. Studies are in progress to measure body temperature and cortisol levels during 24 h to determine whether environmental enrichment affects circadian rhythm or body temperature level.

Both the differences between baseline salivary cortisol concentration and baseline body temperature level between E and P pigs increased with age. Several mechanisms, like development of the HPA-axis and the development of different circadian rhythms, as well as an increased sensitivity to environmental conditions on a certain age, may play a role.

P pigs had a higher cortisol increase in response to relocation than E pigs; however, the area under the response curve after relocation did not differ between E and P pigs. Moreover, the treatments did not differ in the cortisol response to isolation and restraint. Thus, the results indicate that E and P pigs do not differ in their cortisol response to the stressors.

E and P pigs did not differ in the body temperature and heart rate responses to the stressors. Heart rate increased initially in response to all stressors. Body temperature showed an increase in response to relocation and restraint and a slight increase followed by a decrease in response to isolation. The stress-induced hyperthermia in response to restraint in pigs has been described before, and was shown to be mediated by prostaglandin (23); a stress-induced hypothermia has also been described in rats (5). It may be argued that both the body temperature and heart rate responses to

the stressors may have been partially caused by a changed activity. However, during isolation no correlation between the time spent active during the test and the body temperature and heart-rate response was found (data not shown), indicating that the body temperature and heart-rate responses were caused by the stressor only.

CONCLUSIONS

Behavioral measurements in this experiment, although only measured at one stage in development, support the view of other authors (2,3,6,29) that housing pigs in a poor environment has

negative implications for welfare. Surprisingly, enriched-housed pigs had higher baseline cortisol concentrations. Further experiments are needed to determine if environmental enrichment as described in this experiment significantly improves pig welfare.

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